Generating Leslie models

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Introduction

Leslie matrix models, named after Patrick Leslie who introduced them in the 1940s, are a type of matrix population model (MPM) used to describe the demography of age-structured populations. They are commonly used in studies of wildlife, conservation and evolutionary biology.

In a Leslie MPM, the square matrix is used to model discrete, age-structured population growth with a projection interval, most often representing years, as a time step. Each element in the matrix represents a transition probability between different age classes or indicates the average reproductive output (often referred to as fecundity in population biology and fertility in human demography) of the age class. The information in the MPM ($\mathbf{A}$) can be split into two submatrices ($\mathbf{U}$ and $\mathbf{F}$), representing survival/growth and reproduction, respectively. $\mathbf{A} = \mathbf{F} + \mathbf{C}$.

- **Survival Probabilities**: The subdiagonal (immediately below the main diagonal) of the MPM consists of survival probabilities. Each entry here shows the probability that an individual of one age class will survive to the next age class. These probabilities can be understood as an age trajectory of survival that can be modelled using a mathematical model describing how age-specific mortality changes with age.
- **Reproductive Output**: The first row of the MPM contains the reproductive output of each age class, representing the number of new individuals produced in each projection interval. This is often referred to as fecundity in ecological contexts.

All other entries in the MPM are typically zero, indicating that those transitions are impossible.

To project the population size and structure through time, the MPM is multiplied by a vector that represents the current population structure (number of individuals in each age class). This process results in a new vector that shows the predicted structure of the population in the next time step. This calculation can be iterated repeatedly to project population and structure through time.

Leslie matrices are useful for studying population dynamics under different scenarios, such as changes in survival rates, fecundity rates, or management strategies. They have been widely applied in both theoretical and applied ecology.

Aims

The aim of this vignette is to demonstrate how to simulate Leslie matrix population models (MPMs) using functional forms for mortality and reproduction. This simulation is useful for various purposes, including:

- Investigating the influence of senescence parameters on population dynamics.
- Generating MPMs based on empirical parameter estimates of mortality and reproduction from the literature.
- Creating MPMs with specific properties for educational and research purposes.

In the following sections, this document will:

1) Explain the basics of mortality and reproduction trajectories.
2) Show how to produce life tables reflecting trajectories of mortality and reproduction.
3) Show how to produce MPMs from these life tables.
4) Show how to generate sets of many MPMs based on defined mortality and reproduction characteristics.

Preparation

Before beginning, users will need to load the required packages.

```
library(mpmsim)
library(dplyr)
library(Rage)
library(ggplot2)
library(Rcompadre)
```

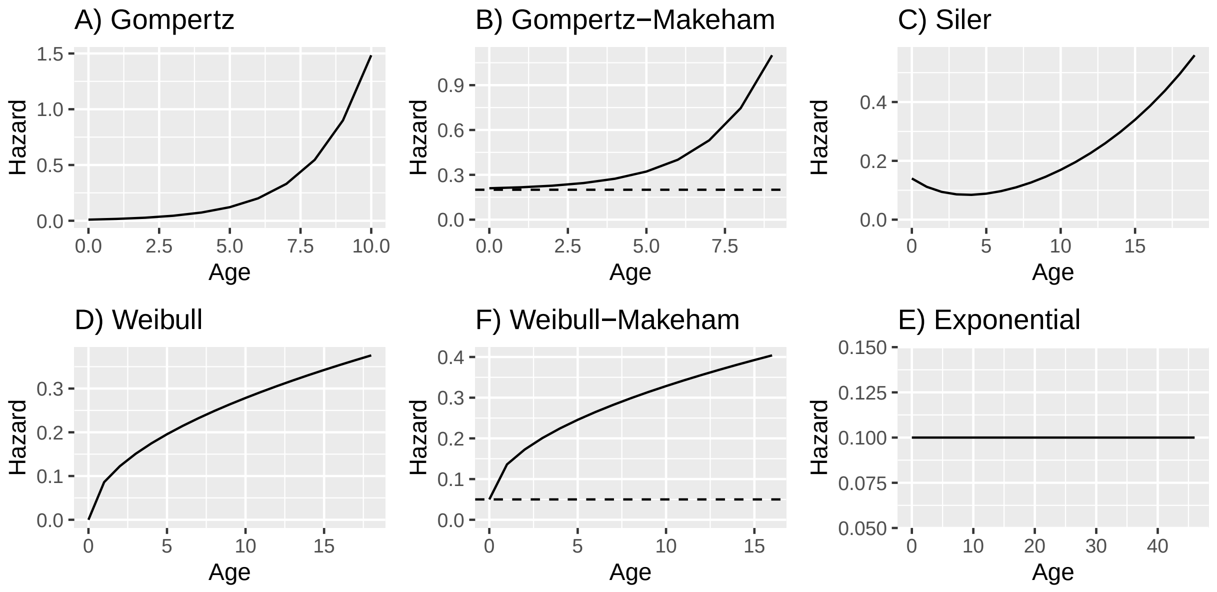
1. Functional forms of mortality and reproduction

There are numerous published and well-used functional forms used to describe how mortality risk (hazard) changes with age. The `model_mortality` function (and its synonym `model_survival`) handles 6 of these models: Gompertz, Gompertz-Makeham, Weibull, Weibull-Makeham, Siler and Exponential.

In a nutshell:

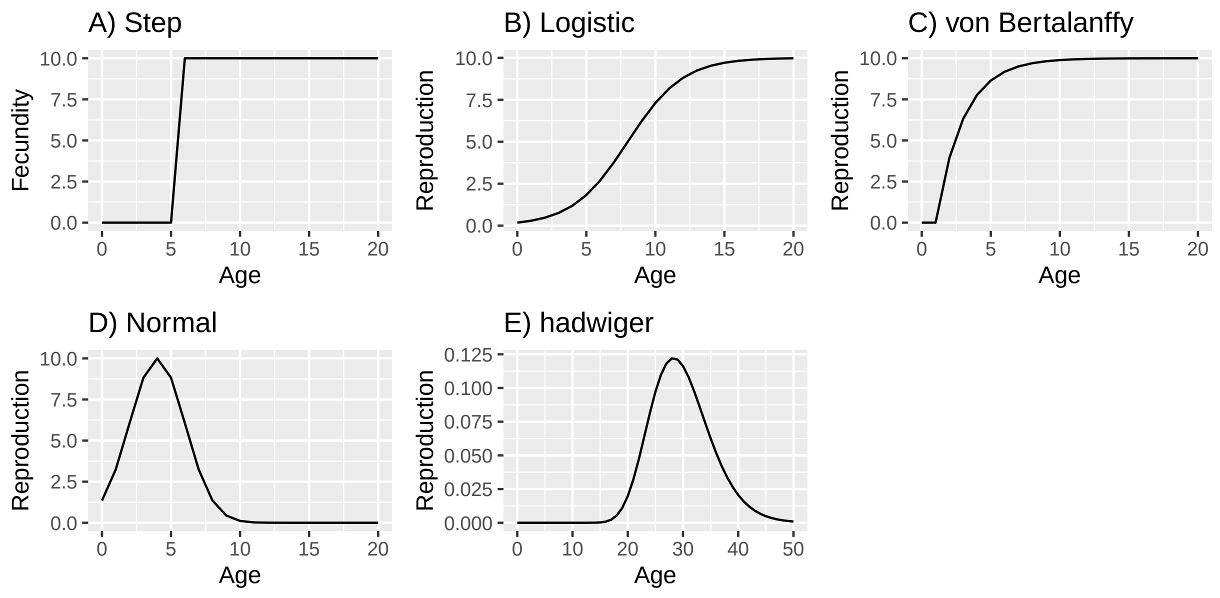
- Gompertz: A mortality rate that increases exponentially with age. $h_x = b_0 \mathrm{e}^{b_1 x}$
- Gompertz-Makeham: A mortality rate that increases exponentially with age, with an additional age-independent constant mortality. $h_x = b_0 \mathrm{e}^{b_1 x} + c$
- Weibull: A mortality rate that scales with age, increasing at a rate that can either accelerate or decelerate, depending on the parameters of the model. $h_x = b_0 b_1 (b_1 x)^{(b_0 - 1)}$
- Weibull-Makeham: as the basic Weibull, but with an additional age-independent constant mortality. $h_x = b_0 b_1 (b_1 x)^{(b_0 - 1)} + c$
- Siler: A mortality model that separates mortality rates into two age-related components — juvenile mortality, which declines exponentially with age and adult mortality, which increases exponentially. $h_x = a_0 \mathrm{e}^{-a_1 x} + c + b_0 \mathrm{e}^{b_1 x}$
- Exponential: Constant mortality that is unchanging with age. $h_x = c$

These are illustrated below.



In addition to these functional forms of mortality, there are, of course, functional forms that have been used to model reproductive output. The `model_fecundity` function (and its synonyms `model_fedundity` and `model_reproduction`) handles five types: logistic, step, von Bertalanffy, normal and Hadwiger. Some of these models originate from human demography, where *fertility* is used for realised reproductive output and *fecundity* refers to reproductive potential. In ecology and population biology, however, *fecundity* typically describes actual reproductive output. Since `mpmsim` is designed for population biologists, we will use the terms *fecundity*, or simply *reproduction/reproductive output*.

- Step: Reproductive output is initially zero, then jumps to a particular level at a specified age, after which it remains constant. $f_x = \begin{cases} A, x \geq m \\ A, x < m \end{cases}$
- Logistic: Reproductive output initially increases rapidly with age then slows to plateau as it approaches a maximum value. $f_x = A/(1 + exp(-k(x - x_m)))$
- von Bertalanffy: This model is often used in growth dynamics but has been adapted for reproduction to describe changes over age or time following a logistic growth form not limited by a strict upper asymptote. It shows how reproductive output might increase and then decrease, following a sigmoid curve. $f_x = A(1 - exp(-k(x - x_0)))$
- Normal : Reproductive output is modelled as normal distribution to describe how reproductive output increases, peaks, and then decreases in a bell curve around a mean age of reproductive capacity. $f_x = A \times \exp\left(-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2\right)$
- Hadwiger: The outcomes of this model are qualitatively similar to the normal distribution. $f_x = \frac{ab}{C}\left(\frac{C}{x}\right)^{\frac{3}{2}} \exp\left\{-b^2\left(\frac{C}{x} + \frac{x}{C} - 2\right)\right\}$



Collectively, these mortality and fecundity functions offer a large scope of options for modelling the variety of demographic trajectories apparent across the tree of life.

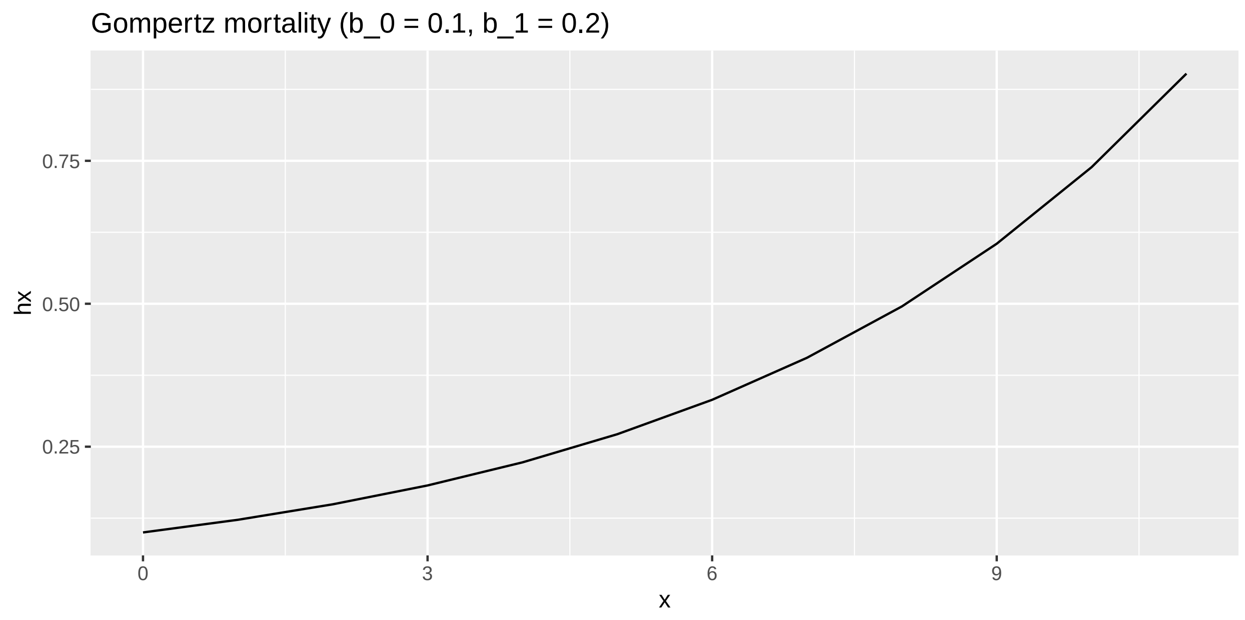
2. Trajectories of mortality and reproductive output, and production of life tables

To obtain a trajectory of mortality, users can use the `model_mortality` function, which takes as input the parameters of a specified mortality model. The output of this function is a standard life table `data.frame` including columns for age (`x`), age-specific hazard (`hx`), survivorship (`lx`, the probability of surviving from birth (age 0) to age `x`), age-specific probability of death and survival (`qx` and `px`). By default, the life table is truncated at the age when the survivorship function declines below 0.01 (i.e. when only 1% of individuals in a cohort would remain alive).

```
(lt1 <- model_mortality(params = c(b_0 = 0.1, b_1 = 0.2), model = "Gompertz"))
#>     x        hx         lx        qx        px
#> 1   0 0.1000000 1.00000000 0.1051240 0.8948760
#> 2   1 0.1221403 0.89487598 0.1268617 0.8731383
#> 3   2 0.1491825 0.78135045 0.1526972 0.8473028
#> 4   3 0.1822119 0.66204041 0.1832179 0.8167821
#> 5   4 0.2225541 0.54074272 0.2190086 0.7809914
#> 6   5 0.2718282 0.42231542 0.2606027 0.7393973
#> 7   6 0.3320117 0.31225886 0.3084127 0.6915873
#> 8   7 0.4055200 0.21595427 0.3626343 0.6373657
#> 9   8 0.4953032 0.13764186 0.4231275 0.5768725
#> 10  9 0.6049647 0.07940180 0.4892807 0.5107193
#> 11 10 0.7389056 0.04055203 0.5598781 0.4401219
#> 12 11 0.9025013 0.01784784 0.6330059 0.3669941
```

It can be useful to explore the impact of parameters on the mortality hazard (`hx`) graphically, especially for users who are unfamiliar with the chosen models.

```
ggplot(lt1, aes(x = x, y = hx)) +
  geom_line() +
  ggtitle("Gompertz mortality (b_0 = 0.1, b_1 = 0.2)")
```

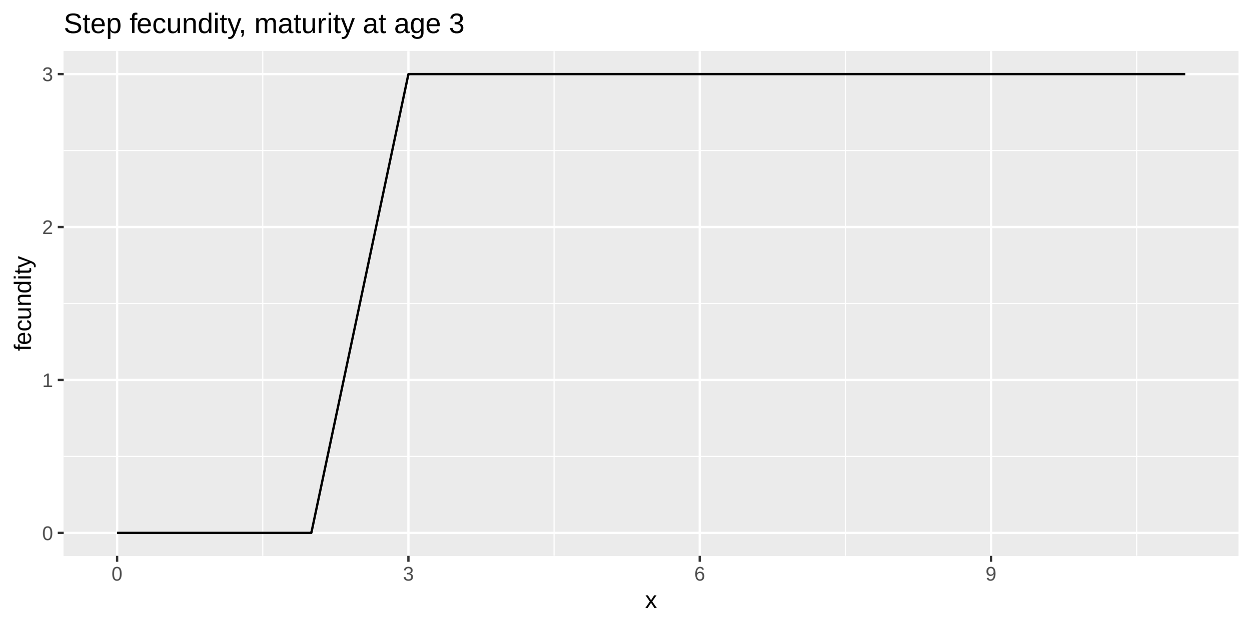


The `model_fecundity` function is similar to the `model_mortality` function, as it has arguments for the type of fecundity model, and its parameters. However, the output of the `model_fecundity` function is a vector of reproductive output values rather than a `data.frame`. This allows us to add a fecundity column (`fecundity`) directly to the life table produced earlier, as follows:

```
(lt1 <- lt1 |>
  mutate(fecundity = model_fecundity(
    age = x, params = c(A = 3),
    maturity = 3,
    model = "step"
  )))
#>     x        hx         lx        qx        px fecundity
#> 1   0 0.1000000 1.00000000 0.1051240 0.8948760         0
#> 2   1 0.1221403 0.89487598 0.1268617 0.8731383         0
#> 3   2 0.1491825 0.78135045 0.1526972 0.8473028         0
#> 4   3 0.1822119 0.66204041 0.1832179 0.8167821         3
#> 5   4 0.2225541 0.54074272 0.2190086 0.7809914         3
#> 6   5 0.2718282 0.42231542 0.2606027 0.7393973         3
#> 7   6 0.3320117 0.31225886 0.3084127 0.6915873         3
#> 8   7 0.4055200 0.21595427 0.3626343 0.6373657         3
#> 9   8 0.4953032 0.13764186 0.4231275 0.5768725         3
#> 10  9 0.6049647 0.07940180 0.4892807 0.5107193         3
#> 11 10 0.7389056 0.04055203 0.5598781 0.4401219         3
#> 12 11 0.9025013 0.01784784 0.6330059 0.3669941         3
```

Again, it can be useful to plot the relevant data to visualise it.

```r
ggplot(lt1, aes(x = x, y = fecundity)) +
  geom_line() +
  ggtitle("Step fecundity, maturity at age 3")
```



3. From life table to MPM

Users can now turn these life tables, containing age-specific survival and reproductive trajectories, into Leslie matrices using the `make_leslie_mpm` function. These MPMs can be large or small depending on the maximum life span of the population: as mentioned above, the population is modelled until less than 1% of a cohort remains alive.

```r
make_leslie_mpm(lifetable = lt1)
#>           [,1]      [,2]      [,3]      [,4]      [,5]      [,6]      [,7]
#>  [1,] 0.000000 0.0000000 0.0000000 3.0000000 3.0000000 3.0000000 3.0000000
#>  [2,] 0.894876 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [3,] 0.000000 0.8731383 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [4,] 0.000000 0.0000000 0.8473028 0.0000000 0.0000000 0.0000000 0.0000000
#>  [5,] 0.000000 0.0000000 0.0000000 0.8167821 0.0000000 0.0000000 0.0000000
#>  [6,] 0.000000 0.0000000 0.0000000 0.0000000 0.7809914 0.0000000 0.0000000
#>  [7,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.7393973 0.0000000
#>  [8,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.6915873
#>  [9,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#> [10,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#> [11,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#> [12,] 0.000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>            [,8]      [,9]     [,10]     [,11]     [,12]
#>  [1,] 3.0000000 3.0000000 3.0000000 3.0000000 3.0000000
#>  [2,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [3,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [4,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [5,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [6,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [7,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [8,] 0.0000000 0.0000000 0.0000000 0.0000000 0.0000000
#>  [9,] 0.6373657 0.0000000 0.0000000 0.0000000 0.0000000
#> [10,] 0.0000000 0.5768725 0.0000000 0.0000000 0.0000000
#> [11,] 0.0000000 0.0000000 0.5107193 0.0000000 0.0000000
#> [12,] 0.0000000 0.0000000 0.0000000 0.4401219 0.3669941
```

4. Producing sets of MPMs based on defined model characteristics

It is sometimes desirable to create large numbers of MPMs with particular properties in order to test hypotheses. For Leslie MPMs, this can be implemented in a straightforward way using the function `rand_leslie_set`. This function generates a set of Leslie MPMs based on defined mortality and fecundity models, and using model parameters that are randomly drawn from specified distributions. For example, users may wish to generate MPMs for Gompertz models to explore how rate of senescence influences population dynamics.

Users must first set up a data frame describing the distribution from which parameters will be drawn at random. The data frame has a number of rows equal to the number of parameters in the model, and two values to describe the distribution. In the case of a uniform distribution, these are the minimum and maximum parameter values, respectively and with a normal distribution they represent the mean and standard deviation. The parameters should be entered in the order they appear in the model equations (see `?model_mortality`), with the exact order depending on the chosen mortality model.

For the Gompertz-Makeham model: $h_x = b_0 e^{b_1 x} + c$

The `output` argument defines the output as one of six types (`Type1` through `Type6`). These outputs include `CompadreDB` objects or `list` objects, and the MPMs can be split into the component submatrices (**U** and **F**, where the MPM, $\mathbf{A} = \mathbf{U} + \mathbf{F}$). In the special case `Type6` the outputs are provided as a `list` of life tables rather than MPMs. If the output is set as a `CompadreDB` object, the mortality and fecundity model parameters used to generate the MPM are included as metadata.

The following example illustrates the production of 50 Leslie MPMs output to a `CompadreDB` object based on the Gompertz-Makeham mortality model and a step fecundity model with maturity beginning at age 0. An optional argument, `scale_output = TRUE` will scale the fecundity in the output MPMs to ensure that population growth rate is lambda. The scaling algorithm multiplies the fecundity part of the MPM (the **F** submatrix) by a simple scaling factor to ensure the population growth rate is 1 while maintaining the shape (but not the magnitude) of the fecundity trajectory. This should be used with care: The desirability of such a manipulation strongly depends on the use the MPMs are put to.

```r
mortParams <- data.frame(
  minVal = c(0, 0.01, 0.1),
  maxVal = c(0.05, 0.15, 0.2)
)

fecundityParams <- data.frame(
  minVal = 2,
  maxVal = 10
)

maturityParam <- c(0, 0)

(myMatrices <- rand_leslie_set(
  n_models = 50,
  mortality_model = "GompertzMakeham",
  fecundity_model = "step",
  mortality_params = mortParams,
  fecundity_params = fecundityParams,
  fecundity_maturity_params = maturityParam,
  dist_type = "uniform",
  output = "Type1"
))
#> A COM(P)ADRE database ('CompadreDB') object with ?? SPECIES and 50 MATRICES.
#>
#> # A tibble: 50 x 8
#>    mat        mortality_model      b_0     b_1      C fecundity_model      A
#>    <list>     <chr>              <dbl>   <dbl>  <dbl> <chr>            <dbl>
#>  1 <CompdrMt> gompertzmakeham 0.0457   0.141  0.129 step              8.64
#>  2 <CompdrMt> gompertzmakeham 0.0321   0.0827 0.174 step              3.08
#>  3 <CompdrMt> gompertzmakeham 0.0328   0.109  0.146 step              7.75
#>  4 <CompdrMt> gompertzmakeham 0.0467   0.0458 0.146 step              9.52
#>  5 <CompdrMt> gompertzmakeham 0.0489   0.0264 0.147 step              6.48
#>  6 <CompdrMt> gompertzmakeham 0.0452   0.0294 0.199 step              9.57
#>  7 <CompdrMt> gompertzmakeham 0.00412  0.0820 0.139 step              9.25
#>  8 <CompdrMt> gompertzmakeham 0.0223   0.127  0.174 step              8.49
#>  9 <CompdrMt> gompertzmakeham 0.0194   0.106  0.100 step              8.66
#> 10 <CompdrMt> gompertzmakeham 0.000367 0.0391 0.191 step              6.89
#> # i 40 more rows
#> # i 1 more variable: fecundity_scaling <dbl>
```

The function operates quite fast. For example, on an older MacBook (3.10GHz Intel with 4 cores), it takes 17 seconds to generate 5000 MPMs with the parameters mentioned above.

As an aid to assessing the simulation, users can produce a simple summary of the MPMs using the `summarise_mpms` function. Note, though, that this only works with `CompadreDB` outputs. In this case, because we are working with Leslie MPMs, the dimension of the MPMs is indicative of the maximum age reached by individuals in the population.

```
summarise_mpms(myMatrices)
#> Summary of matrix dimension:
#>    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
#>   15.00   18.25   22.00   22.98   26.00   39.00
#> Summary of lambda values:
#>    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
#>   2.845   6.010   7.970   7.557   9.150  10.672
#>
#> Summary of maximum F values:
#>    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
#>   2.002   5.157   7.142   6.720   8.327   9.788
#>
#> Summary of maximum U values:
#>    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
#>  0.7829  0.8159  0.8347  0.8365  0.8545  0.8925
#>
#> Summary of minimum non-zero U values:
#>    Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
#>  0.5715  0.6881  0.7650  0.7514  0.8160  0.8814
```

After producing the output as a `CompadreDB` object, the matrices can be accessed using functions from the

RCompadre R package. For example, to get the A matrix, or the U/F submatrices users can use the matA, matU or matF functions. The following code illustrates how to rapidly calculate population growth rate for all of the matrices.

```
# Obtain the matrices
x <- matA(myMatrices)

# Calculate lambda for each matrix
sapply(x, popdemo::eigs, what = "lambda")
#>  [1]  9.480062  3.889616  8.587381 10.343567  7.303660 10.356146 10.112353
#>  [8]  9.308862  9.549256  7.720332 10.672096  7.928430  5.604869  8.872518
#> [15]  6.966830  7.339943  9.468459  3.993036  8.631979  2.871674  8.012464
#> [22]  3.567593  2.844529  8.688251  7.778629  5.968972  8.664013  9.523154
#> [29]  7.123514  9.482587  7.556071 10.495633  7.644149  7.441366  7.792883
#> [36]  9.092281 10.412818  5.422186  9.018497  8.325535  4.386485  5.377892
#> [43]  6.131147  3.940014  8.952296  4.907484  9.138780  9.154187  3.317446
#> [50]  8.668165
```

Users can examine the vignettes for the Rcompadre and Rage packages for additional insight into other potential operations with the compadreDB object.

Conclusion

This vignette demonstrated how to generate Leslie matrices using functional forms of mortality and fecundity, allowing users to simulate virtual species with varied life histories. These matrices can be used to explore how life history or parameter differences affect population dynamics, supporting various research and educational applications.